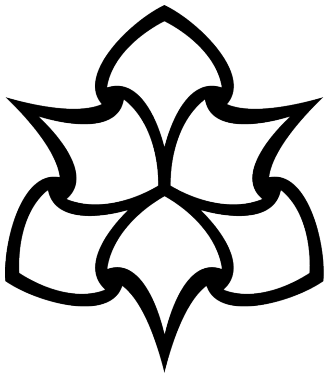


LRH: Brearley

RRH: Dipterocarpaceae Mycorrhizas

Ectomycorrhizal Associations of the Dipterocarpaceae

Francis Q. Brearley [1]

School of Science and the Environment, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD, U.K.

Received 16 April 2011; revision accepted 10 October 2011.

[1] Corresponding author; e-mail: f.q.brearley@mmu.ac.uk

ABSTRACT

Dipterocarps are one of the most important tree families in the lowland forests of Southeast Asia and are somewhat unusual among tropical trees in that they form ectomycorrhizal (EcM) symbiotic root-inhabiting fungal associations. It has been hypothesised that dipterocarps have been partnered in this mutualistic association prior to the separation of Gondwana. Under many conditions EcMs form rapidly on dipterocarp seedlings through inocula present in the soil, although few studies have been conducted to provide evidence that they improve seedling establishment and performance. There are hundreds of EcM species associated with dipterocarps. Fungal fruit body surveys suggest the most important families are Amanitaceae, Boletaceae and Russulaceae, although Thelephoraceae also become numerically important when root tips are examined. EcM communities are affected by various biotic and abiotic factors, as well as anthropogenic perturbations, and I examine the importance of these in structuring EcM communities.

Key words: fungi; mycorrhiza; molecular identification; mutualism; seedling performance; soils; symbiosis.

LOWLAND EVERGREEN RAIN FORESTS OF SOUTHEAST ASIA ARE HIGHLY SPECIES RICH. Their tree communities are dominated by members of the Dipterocarpaceae (Proctor *et al*. 1983, Newman *et al*. 1996, 1998; Brearley *et al*. 2004, Slik *et al*. 2009). In addition to their ecological dominance, dipterocarps also provide significant economic resources, producing not only valuable timber, but also a number of non-timber forest products such as oils, nuts and resins (Shiva & Jantan 1998). With continued degradation of forests in the Southeast Asian region, there is an increased interest in establishing plantations of forest trees and promoting restoration strategies (Kettle 2010). Due to their important ecological and economic roles, understanding the growth and regeneration of dipterocarps is an important research priority. The role of light and nutrients in seedling growth and performance has received much attention in this regard; that of mycorrhizas has often been invoked but much less studied.

Mycorrhizas are an intimate symbiotic association between specialised root-inhabiting fungi and the roots of living plants; they are generally considered mutualistic as benefits are accrued by both partners. The plant provides the fungus with carbon derived from its photosynthetic activity and, in return, the fungus can improve nutrient uptake, growth, water relations, pathogen and heavy metal resistance of the plant (van der Heijden & Sanders 2002, Smith & Read 2008, and references therein). Mycorrhizas are important as they extend roots' nutrient depletion zones, especially for poorly mobile inorganic nutrients such as phosphorus (P) that are found at especially low concentrations in many tropical soils (Proctor *et al*. 1983, Brearley 2003, Brearley *et al*. 2004, Paoli *et al*. 2006). Early work on mycorrhizas focused on this nutrient uptake capability of the symbiosis but we are now aware of the multifunctional role played by mycorrhizas in enhancing protection against a number of environmental stresses, and it is clear that this role acts

47 independently of improved plant nutrition (Read 1986, Newsham *et al*. 1995). This led
48 Read (1998) to propose a definition of mycorrhizas as 'structures in which a symbiotic
49 union between fungi and plant roots leads to increases in fitness of one or both
50 partners'. An estimated 95 percent of plant species are in characteristically mycorrhizal
51 families (Read 1999) and they are found in almost every terrestrial ecosystem. The
52 arbuscular mycorrhizal (AM) symbiosis, formed by members of the Glomeromycota, is
53 the most abundant type of mycorrhiza, and most tropical trees form AMs (de Alwis &
54 Abeynayake 1980, St. John 1980, Chalermpongse 1987, Newbery *et al*. 1988,
55 Moyersoen 1993, Béreau *et al*. 1997, McGuire *et al*. 2008). An important, and often
56 dominant, minority of tropical tree families, including the Dipterocarpaceae, form EcMs
57 (Figure 1) that are mostly members of the Basidiomycota or Ascomycota. EcM trees in
58 the tropics often form monodominant stands (Connell & Lowman 1989, Henkel 2003,
59 Peh *et al*. 2011) but the dipterocarps rarely do so.
60
61 In this review, I outline the current state of knowledge of dipterocarp EcM fungi and
62 their role in tropical ecosystems. The vast majority of current work is from the Asian
63 dipterocarps and studies on these species, therefore, form most of the body of this
64 review. I focus on the role of EcMs in improving seedling growth and performance (see
65 also Brearley 2011), and on EcM species diversity and factors affecting patterns of
66 diversity. I start with a brief history of dipterocarp mycorrhizal research and the
67 biogeographical insights it has provided. I then examine the role of EcMs in the growth
68 and performance of dipterocarp seedlings under both nursery and field conditions. The
69 range of fungal species that form EcMs on dipterocarps is then explored, and I outline
70 the how new molecular techniques have improved our knowledge of dipterocarp EcMs.
71 Key determinants of EcM community dynamics, including various biotic and abiotic

72 factors and perturbations, are then evaluated. Colonization by other symbiotic fungi is
73 briefly assessed. The review concludes with some thoughts on future research priorities.
74
75 **BRIEF HISTORY OF DIPTEROCARP MYCORRHIZAL RESEARCH**
76 Van Roosendael and Thorenaar (1924) and de Voogd (1933) both noted the presence of
77 'mycorrhizas' on the roots of dipterocarp seedlings although it is not clear exactly what
78 they saw as they did not publish pictures or record further observations. Although John
79 Corner (1972, among others) noted EcM fungal fruiting bodies in dipterocarp forests, he
80 attributed this to the presence of the Fagaceae (long known to be EcM in temperate
81 regions), and it was not until 1966 that Singh recorded that dipterocarps, in common
82 with a few other tropical angiosperms (Peyronel & Fassi 1957), formed EcMs. Early
83 work (1960s to 1980s) simply noted various dipterocarp species as forming EcM
84 associations (Singh 1966, de Alwis & Abeyneyake 1980, Alexander & Högberg 1986)
85 and made cursory attempts to ascertain which fungal species were putative EcM formers
86 (Hong 1979). The first attempts at *in vitro* synthesis of EcMs were not reported until the
87 late 1980s (Louis & Scott 1987, de Alwis & Abeyneyake 1988) along with early reports
88 of increased growth of inoculated seedlings also around this time (Hadi & Santoso
89 1988, Santoso 1988). In the late 1980s and early 1990s, Lee Su See's work advanced
90 EcM research by examining functional aspects of the symbiosis *e.g.,* interactions of
91 EcMs with nutrients to determine seedling growth (Lee & Alexander 1994), and the
92 succession of EcM fungi on seedlings (Lee & Alexander 1996) and her collaborations
93 with Frédéric Lapeyrie advanced inoculation techniques with a range of fungal species
94 (Yazid *et al*. 1994, 1996; Lee *et al*. 1995b, 2008). Throughout the 1990s to mid 2000s
95 the IUFRO-SPDC funded BIO-REFOR conferences led to more work being published
96 in the region; although some of these papers were valuable, many had limited value due

97 to inappropriate design or lack of detail in reporting (Brearley 2011). The involvement
98 of Roy Watling in the 1990s started to build knowledge of the fungal flora of Peninsular
99 Malaysia from the strong foundations laid by Corner (Watling & Lee 1995, 1998, 2007;
100 Watling *et al*. 1995a, 1998, 2002, 2006; Lee *et al*. 2002a, 2003; Lee 2005).
101 Subsequent eco-physiological work examined how EcM communities were affected by
102 biotic and abiotic perturbations (Brearley 2006, Brearley *et al*. 2003, 2007) and
103 examined the role of EcMs in organic nitrogen acquisition (Brearley *et al*. 2003). The
104 first molecular study of dipterocarp EcM communities appeared in 2003
105 (Sirikantaramas *et al*. 2003), and since then there have been a few more (Moyerseon
106 2006, Yuwa-Amornpitak *et al*. 2006, Tedersoo *et al*. 2007a, Peay *et al*. 2010) although
107 until the comprehensive study by Peay *et al*. (2010) these had mostly focused on rare or
108 outlying members of the Dipterocarpaceae. Most recently, advances based on early
109 nursery-based inoculation studies have been extended to the field performance of
110 dipterocarp seedlings (Brearley 2003, Turjaman *et al*. 2007, Lee *et al*. 2008, Tata *et al*.
111 2010).
112
113 **INSIGHTS FROM ECTOMYCORRHIZAS INTO THE ORIGINS AND**
114 **BIOGEOGRAPHY OF THE DIPTEROCARPACEAE**
115 The biogeography of the Dipterocarpaceae is interesting as the vast majority of the 520
116 or so species are found in Southeast Asia with around 30 species in Africa and two in
117 South America (Dayanandan *et al*. 1999). The consistent EcM status of
118 Dipterocarpaceae in Southeast Asia, the dipterocarp sub-family Monotoideae in Africa
119 and the Neotropical genus *Pakaraimaea*, suggests a common EcM ancestor and
120 evolution of the EcM habit before continental separation of Gondwana. Doucousso *et*
121 *al*. (2004) placed the origin of the EcM habit at least 88 million yr ago, prior to the

separation of Madagascar and India, as the closest relative of the Dipterocarpaceae sharing a common ancestor, the Madagascan Sarcoleanaceae, are also EcM. The more recent discovery by Moyersoen (2006) that *Pakaraimaea dipterocarpacea*, basal in the dipterocarp clade, is also EcM suggests an earlier origin of the EcM habit to around 135 million yr ago before the continental separation of South America from Africa. This predates the earliest EcM fossils, which are around 50 million yr old (LePage *et al*. 1997, Beimforde *et al*. 2011) and sets the evolution of the EcM habit on the same timescale as the rise and radiation of the angiosperms. The evidence is not conclusive, however, as Alexander (2006) suggests that the Dipterocarpaceae might not have been EcM prior to the separation of the continents but became EcM at a later stage.

EFFECTS OF ECTOMYCORRHIZAL COLONIZATION ON THE GROWTH AND PERFORMANCE OF DIPTEROCARP SEEDLINGS

The importance of EcMs for dipterocarp seedling growth and performance has been reviewed recently (Brearley 2011) and so this topic is only briefly addressed here. Numerous nursery experiments show that EcMs improve dipterocarp seedling growth and nutrient uptake (Hadi & Santoso 1988, 1989; Santoso 1988, 1991; Lee & Alexander 1994; Yazid *et al*. 1994, 1996; Turjaman *et al*. 2005, 2006; Lee *et al*. 2008) and facilitate access to organic N sources (Brearley *et al*. 2003). These experiments have often been conducted with exotic EcM isolates, as it has proved difficult to isolate fungi from fruit bodies found in Southeast Asian forests. Simple observations and experiments have also correlated seedling biomass (Turner *et al*. 1993), relative growth rates (Saner *et al*. 2011) and foliar P concentrations (Lee & Lim 1989) with percentage EcM colonization. It should be reiterated, however, that most of the above experiments

146 have been conducted under controlled nursery conditions, sometimes with only a single
147 species of EcM inoculated onto the roots of the experimental seedlings.
148
149 Experiments under field conditions are rarer and seedlings do not show as clear a
150 response to the presence of EcMs when planted in natural forest or rubber agroforest
151 (Brearley 2003, Tata *et al*. 2010). For example, there was no clear biomass response of
152 *Hopea nervosa* and *Parashorea tomentella* seedlings to a reduction in EcM colonization
153 by fungicide addition, though foliar nutrient concentrations did show a decline (Brearley
154 2003). There are significant challenges, however, in conducting field experiments, the
155 major one being that it is very difficult to create truly non-mycorrhizal controls.
156 Similarly, for inoculation experiments, such as that of Tata *et al*. (2010), where EcM
157 inoculum is already present in the soil, the benefits of inoculating seedlings are not
158 clear, especially if the inoculated EcM species does not remain on the roots of the
159 seedlings. In contrast, the work of Turjaman *et al*. (2007) in degraded peat swamp forest
160 did show improved growth of inoculated dipterocarp seedlings when out-planted in a
161 degraded peat swamp area. This suggests that EcMs are most likely to benefit seedling
162 performance when seedlings are planted in degraded areas where suitable EcM
163 inoculum is not available, such as mine tailings (Lee *et al*. 2008), burnt areas (Akema *et*
164 *al*. 2009), degraded peatlands (Turjaman *et al*. 2007) or areas previously used for
165 agriculture (Ingleby *et al*. 2000). In many cases, such as in logged forest, EcM
166 colonization occurs rapidly and naturally (Lee & Alexander 1996, Lee *et al*. 1996b) and
167 under such conditions inoculation might not be worthwhile (Brearley 2011).
168 Furthermore, inoculated EcM species do not always remain on the seedling roots, for
169 example Chang *et al*. (1994, 1995) showed that a species of *Pisolithus* in Malaysian

170 inoculation experiments had mostly disappeared from roots six months after colonised
171 seedlings were planted into the field.
172
173 Clearly, we need to further evaluate the growth and survival of EcM *versus* non-EcM
174 seedlings in the field, as positive responses to EcMs in simplified nursery environment
175 are unlikely to be representative of those found in forest sites. In addition, we need an
176 effective way to create truly non-mycorrhizal control seedlings for comparisons with
177 experimental seedlings.
178
179 **NURSING ROLE OF PARENT TREES**
180 Early colonization of dipterocarps is dependent upon mycorrhizal connections made
181 with parent trees (Alexander *et al*. 1992), but the importance of these connections for
182 carbon transfer between plants *via* hyphal connections of non host-specific fungi, which
183 has been demonstrated by Simard *et al*. (1997) in boreo-temperate forests, is not clear.
184 Potentially, movement of compounds through hyphal connections could provide an
185 important carbon subsidy to maintain dipterocarp seedlings in a light-limited state in the
186 forest understory. Two experiments conducted in Malaysian Borneo have shown that
187 inter-individual connections by EcM hyphal networks do not appear to influence
188 dipterocarp seedling growth (Brearley 2003, Saner 2009). These results contrast with
189 that of McGuire (2007) who found that incorporation into an EcM hyphal network was
190 important for seedling growth in a similarly EcM-dominated forest of Guyana.
191 Differences among these forest systems could be related to the differences in tree
192 diversity between the sites, with a monodominant stand in Guyana compared with the
193 high-diversity sites in Southeast Asia. Where there are many EcM parent trees

194 belonging to different species, as in Southeast Asia, supporting heterospecific seedlings
195 with carbon compounds may well be selected against.
196
197 **FUNGAL FLORAS AND NEW FUNGAL SPECIES**
198 The fungal flora of most dipterocarp forests is still very poorly known. Hong (1979)
199 made the first note of putative EcM fungi including *Amanita*, *Boletus*, *Gyrodon*,
200 *Lactarius* and *Russula* species from around dipterocarps at the Forest Research Institute
201 of Malaysia's grounds at Kepong, Peninsular Malaysia. Malaysia is probably one of the
202 best-documented tropical countries in terms of its fungal flora but, even here, it is
203 estimated that only 20 percent of the Peninsula's larger fungi have been collected
204 (Corner, in Lee *et al*. 1995a).
205 The main site where detailed fruit body surveys have been carried out is Pasoh Forest
206 Reserve in Peninsular Malaysia where Lee Su See, Roy Watling and colleagues have
207 been working since the early 1990s (Lee *et al*. 2002a, 2003; Watling *et al*. 1998, 2002,
208 2006). From these surveys, we know that the most common families found as fruiting
209 bodies are Russulaceae, Boletaceae and Amanitaceae, and 296 species of fruiting body
210 (in 19 predominantly EcM-forming families) have been recorded over a six-yr period
211 (Lee *et al*. 2003). Around two-thirds of these were undescribed, and over three-quarters
212 of the species were only collected once. Good information on fungal communities is
213 also available from planted dipterocarps at Kepong, Peninsular Malaysia (Lee *et al*.
214 1996a, Watling & Lee 1995, 1998) and natural forest at Wanariset Samboja,
215 Kalimantan (Smits 1994, Yasman 1995) and from Corner's early work in Malaysia and
216 Singapore (Corner 1988).
217 The fruiting bodies in the more seasonal dipterocarp forests of Thailand are broadly
218 similar at the family level to those in Malaysia and Indonesia, with addition of *Astraeus*

(Chalermpongse 1987) that appears to be absent from the more aseasonal forests. There are also minor fungal inventories from Uppangala in the Western Ghats of India (Natarajan *et al*. 2005) and Sakaerat in Thailand (Chalermpongse 1987) which show similar patterns to the more extensive inventories. López-Quintero *et al*. (in press) have provided the first records of EcM fruiting bodies associated with the Neotropical dipterocarp *Pseudomonotes tropenbosii* in Colombia.

DESCRIPTIONS OF DIPTEROCARP-ASSOCIATED ECTOMYCORRHIZAS

There are very few published descriptions of dipterocarp EcMs and this hinders research for ecologists and mycologists who lack access to molecular sequencing facilities. Becker (1983) and Lee (1988, Lee *et al*. 1997) described over 25 EcM morphotypes from the roots of *Shorea leprosula*, and this is currently the most comprehensive set of dipterocarp EcM descriptions that we have. Watling *et al*. (1995a) described the EcM formed by *Pisolithus aurantioscabrosus*, Tedersoo *et al*. (2007a,b) described the EcMs formed by Sordariomycete and *Coltriciella* species on *Vateriopsis seychellarum* and Jülich (1985) described the distinctive EcMs of *Riessia* and *Riessiella* with abundant cystidia (noted as conidia by Jülich: 1985), with Lee *et al*. (1997) showing how these particular species differ from many EcMs in lacking a Hartig net. Lee *et al*. (2010) also described a new Thelephoraceae species (FP160; most probably *Tomentella*) used in Malaysian inoculation trials.

MOLECULAR STUDIES ON DIPTEROCARP-ASSOCIATED ECTOMYCORRHIZAS

Two of the most comprehensive studies of dipterocarp EcM communities have, ironically, been conducted on rare or outlying species within monospecific genera.

244 Moyersoen (2006) found nine EcM species on *Pakaraimea dipterocarpacea* in
245 Venezuela, and Tedersoo *et al*. (2007a) found 18 EcM species on *Vateriopsis*
246 *sechellarum* in the Seychelles. In Malaysian forests, Sirikantaramas *et al*. (2003) took
247 root samples from five sites and showed that, belowground, the family producing the
248 greatest number of sequences was the Thelephoraceae with just over half of the
249 sequences. Other important families were Boletaceae, Russulaceae and
250 Sclerodermataceae. Numerically this was similar to the results of Yuwa-Amornpitak *et*
251 *al*. (2006) who obtained sequences from root tips from eight sites in Thailand and
252 found, again, Thelephoraceae to provide the greatest number of sequences followed by
253 Russulaceae and Sclerodermataceae. Sirikantaramas *et al*. (2003) also suggested that
254 Thelephoraceae were often found associated with *Shorea* species but did not present
255 further evidence to support their case. Currently, the most comprehensive study we have
256 is that of Peay *et al*. (2010) who examined EcMs in two soil types at Lambir Hills in
257 Sarawak and found that members of the Russulales represented around one-third of the
258 sequences, and the Thelephorales were the fourth most abundant clade (after Boletales
259 and Agaricales). In a dry dipterocarp forest in Thailand, Phosri *et al*. (in press) found
260 Russulales and Thelephorales to be the most important taxa. In addition, Roy *et al*.
261 (2009) determined that EcM fungi were associated with three Thai orchid species (two
262 from forests with dipterocarps). These orchids are highly likely to be obtaining carbon
263 subsidies from the associated dipterocarps. Numerically important fungal groups
264 associated with these orchids were Thelephoraceae, Russulaceae, Clavulinaceae and
265 Sebacinales. Tedersoo *et al*. (2011) have also noted the important EcM species in two
266 African forests containing dipterocarps as non-dominant species. Table 1 summarises
267 the importance of various fungal groups in the studies above with some additional
268 studies also reported.

Tedersoo and Nara (2010) suggest that tropical regions have lower EcM species diversity than temperate regions due to reduced phylogenetic diversity of host trees, and a simpler soil profile, among other reasons. It is difficult, however, to reconcile this suggestion with the very high diversity of fruit bodies collected by Lee *et al*. (2003) as noted above, especially as belowground diversity has been shown to be higher than aboveground diversity in tropical forest EcM fungal surveys (Henkel *et al*. in press); clearly more work is needed to resolve this problem.

ECTOMYCORRHIZAL COMMUNITY DIVERSITY, DYNAMICS AND RESPONSES TO PERTURBATIONS

On *Shorea leprosula*, Lee *et al*. (1997) described 24 EcM morphotypes from various sites in Peninsular Malaysia and 36 at Danum Valley in Borneo (Lee *et al*. 1996b), Ingleby *et al*. (1998) found a similar number (26) on the roots of *Shorea parvifolia* as did Moyersoen (2000) on *Shorea pachycarpa* (29). A much higher richness of 56 EcM morphotypes were found on *Hopea nervosa* at Danum Valley (Lee *et al*. 1996b). The number of EcM morphotypes found in two nursery studies (14 and 16 species, Brearley 2003 and Saner *et al*. 2011 respectively) appears to be lower than the field studies as many late-stage fungi (*sensu* Deacon *et al*. 1983) will be absent from nurseries. Individual seedlings may possess up to five different EcM morphotypes with 2–3 being the median number (Lee & Alexander 1996, Brearley *et al*. 2003). A succession of EcM fungi was observed on *Shorea leprosula* seedling root tips during early seedling establishment, and the number of morphotypes increased over the first seven months of seedling growth (Lee & Alexander 1996). Comparisons between seedling EcM communities will therefore be sensitive to seedling age.

294

295 Studies on the population structure of dipterocarp EcMs appear to be limited to a single
296 study. Rivière *et al*. (2006) examined the spatial distribution of a *Russula* species in
297 dipterocarp forests dominated by *Vateria indica* and *Dipterocarpus indicus* in the
298 Western Ghats of India. The fruiting bodies were highly aggregated but, using
299 molecular methods, genet size was shown to be vary variable, ranging from a number of
300 single fruiting body genets, to the largest genet containing three fruiting bodies with a
301 maximum distance of 70 m between them. These data suggest that *Russula* species can
302 form large genets, in contrast to earlier work that has shown *Russula* species to form
303 relatively small genets (Redecker *et al*. 2001, Liang *et al*. 2004).
304

305 HOST SPECIFICITY.— Smits (1983, 1985) provided anecdotal evidence suggesting that
306 dipterocarp associated EcMs are highly host specific. Unfortunately, due to the lack of
307 methodology presented in his papers it makes them difficult to evaluate. Furthermore,
308 these results do not agree with those found in temperate regions where many fungi have
309 an intermediate to broad host range, certainly at the host genus taxonomic level or
310 above (Molina *et al*. 1992). Current evidence suggests that host specificity of
311 dipterocarp EcMs is not as common as claimed by Smits (1983, 1985) with weak
312 evidence for host specificity provided by Ingleby *et al*. (2000) who showed that
313 seedlings of *Dipterocarpus alatus* grown in soil from a *Hopea odorata* plantation in
314 Vietnam formed only one EcM morphotype, and this was different to the four
315 morphotypes on *Hopea odorata* seedlings. Becker (1983) described ten EcM
316 morphotypes from *Shorea leprosula* and *Shorea maxwelliana* at Pasoh of which two
317 were shared between the two hosts. Similarly, Berriman (1986) showed that three out of
318 11 morphotypes were shared between three *Shorea* seedling species (*Shorea leprosula*,

319 *Shorea lepidota* and *Shorea macroptera*) and seven were found on only one of the
320 species. In nursery-grown dipterocarp seedlings, seven of 14 EcM morphotypes found
321 were present on the roots of at least three of the four host seedling species of
322 *Dryobalanops lanceolata*, *Hopea nervosa*, *Parashorea tomentella* and *Shorea leprosula*
323 (Brearley *et al*. 2003, 2007). Lee *et al*. (1996b) recorded 61 EcM morphotypes on the
324 roots of seedlings of *Hopea nervosa* and *Shorea leprosula* in forests at Danum Valley in
325 Sabah, of which 31 were found on both species, 25 were found on *Hopea nervosa* only,
326 and only five were found exclusively on *Shorea leprosula*. Examination of associations
327 of fruit bodies with planted dipterocarp species suggests that *Russula virescens* is
328 putatively associated with at least ten dipterocarp species and *Boletus aureomycelinus*
329 with 21 species (Watling and Lee 1998). All of the above evidence suggests a modest
330 amount of host specificity although the degree to which this simply represents random
331 sampling of rare species can only be ascertained with more extensive sampling.
332 At a higher taxonomic level, two dipterocarp-associated EcM fungi (*Pisolithus*
333 *aurantioscabrosus* and *Tomentella* FP160) have also been shown to form EcMs on
334 *Acacia mangium* although it is not yet known if these are functionally important (Lee &
335 Patahayah 2003). Of the 18 species of EcM fungi on *Vateriopsis seychellarum*, three
336 were shared with *Intsia bijuga*, and another three were shared with introduced
337 *Eucalyptus robusta* (Tedersoo *et al*. 2007a). As a long-isolated island endemic
338 (occurring only on a single island of the Seychelles) and an evolutionary basal lineage,
339 *V. seychellarum* might not, however, be very representative of the Asian dipterocarps in
340 this respect.
341
342 REPONSES TO NUTRIENT AVAILABILITY.— Many studies show that mycorrhizal
343 colonization decreases under conditions of higher soil, and especially P, fertility (Jones

344 *et al*. 1990, Baum & Makeschin 2000, Treseder 2004) but the results from dipterocarps
345 are variable. Turner *et al*. (1993) found that NPK fertilization increased percentage EcM
346 colonization on *Shorea macroptera* seedlings, and the correlation between percentage
347 EcM and seedling biomass was stronger if the unfertilised seedlings were analysed
348 alone. Similarly, Lee and Lim (1989) found that only seedlings from a less fertile site
349 had a correlation between percentage EcM colonization and foliar P concentrations.
350 Irino *et al*. (2004) showed that addition of a NPK fertilizer increased EcM colonization
351 on pot-grown *Dryobalanops lanceolata*, although colonization was very low (8%) in the
352 control seedlings. In contrast, addition of P in various studies had no effect on % EcM
353 on *Shorea leprosula* (Suhardi 2000), two species of *Dryobalanops* in two contrasting
354 soil types (Palmiotto *et al*. 2004), or on *Hopea nervosa* and *Shorea leprosula* (Brearley
355 *et al*. 2007). However, the latter study did find species-specific responses to increased
356 nutrient availability, most notably for *Riessiella* sp. that increased following P
357 fertilization. This suggests that *Riessiella* might not be a fully mutualistic fungus
358 (Brearley *et al*. 2007); further evidence for this hypothesis is that it also does not
359 possess a Hartig Net (Lee *et al*. 1997), which is the site of nutrient transfer between the
360 fungus and the plant. The lack of a consistent response to P fertilization in these studies
361 suggests that EcMs are important even under conditions of higher nutrient supply as
362 colonization rarely declines, suggesting they are still involved in assisting in seedling
363 nutrient uptake.
364
365 When an organic nutrient source of mixed leaf litter was added to the soil medium there
366 was no change in percentage EcM colonization for three dipterocarp seedling species
367 (Brearley *et al*. 2003). In contrast, the diversity of EcM species on seedling's roots was
368 reduced with litter addition; this was partly driven by the reduction in colonization by

Cenococcum geophilum. Addition of *Imperata cylindrica* (alang-alang) litter reduced percentage EcM colonization in *Shorea bracteolata* (Suhardi *et al*. 1993), perhaps due to its allelopathic nature (Brook 1989).

RESPONSES TO SOIL TYPES .—The EcM community on the roots of nursery-grown *Dryobalanops lanceolata* is considerably different when seedlings are grown on ultramafic (with high levels of metals such as Fe, Mg, Ni, Co and Cr) as compared to a more typical non-ultramafic ultisol soil (Brearley 2006), notably in that *Cenococcum geophilum* and *Inocybe* spp. decreased, and *Boletales* sp. increased in ultramafic soils, and EcM diversity was also higher. Similarly, Iwamoto and Kitayama (2002) found eleven EcM morphotypes in ultramafic soil compared to only two in a sedimentary soil from dipterocarp-dominated forests at around 700 m asl on Mount Kinabalu in Borneo.

Sandy soils at Lambir Hills, Sarawak, had a greater number of EcM species than clay soils (65 *vs*. 41), perhaps due to more differentiated soil horizons of the sandy soils or the lower nutrient concentrations, allowing coexistence of a greater number of species (Peay *et al*. 2010). Such results might also, however, be due to different tree compositions on the different soil types. There was also evidence of more phylogenetic clustering of EcM species on the clay soil, giving rise to a community more dominated by Russulales and Thelephorales and lacking Cortinariaceae. Seedlings of *Dryobalanops lanceolata* (but not *D. aromatica*) at Lambir Hills had more than double the biomass of EcM when grown on their preferred soil type (clay and sandy soils respectively; Palmiotto *et al*. 2004)

393 REPONSES TO IRRADIANCE.— Studies examining changes in EcM colonization in
394 response to differing irradiances are somewhat contrasting, most likely this is due to
395 changes in carbohydrate flow from plant to fungus but will also be due to the differing
396 environmental conditions associated with higher irradiance, such as higher soil
397 temperatures. High light conditions (e.g. in forest gaps) appear to increase EcM
398 colonization (Becker 1983; Ingleby *et al*. 1998). EcM colonization on five Sri Lankan
399 *Shorea* species was also greatest under higher irradiances, often under full sunlight,
400 even though this did not correspond to conditions most suited to seedling growth of
401 these species (Tennakoon *et al*. 2005). In contrast, Yasman (1995) found the greatest
402 EcM colonization under irradiances where seedling growth was also most rapid, while
403 other studies have shown no clear difference among different light treatments of EcM
404 abundance on seedlings of two contrasting species, *Shorea leprosula* and *Hopea*
405 *nervosa* (Brearley *et al*. 2007). When considering diversity of EcMs under differing
406 conditions we may also need to examine the size of the root system and the number of
407 root tips present, as, analogous to a species-area effect, larger root systems with more
408 root tips may well host more EcM species (see Taylor 2002).
409
410 RESPONSES TO BURNING.— Tata *et al*. (2003) did not find any EcM fruit bodies in
411 forests burnt in 1998 in East Kalimantan (examined in 2000) and, using two dipterocarp
412 seedling species as bait plants, she found there was no difference in the proportion of
413 seedlings with EcM (although values for both species were low at around 5%) among
414 seedlings grown in the burnt and unburnt forest soils. In contrast, Akema *et al*. (2009)
415 found that in a severely burnt site (examined in 2002) there were no EcM root tips in the
416 soil, although there were some fruiting bodies of typically early stage fungi (*Laccaria*
417 *vinaceoavellana*). In the moderately burnt site, four EcM morphotypes were found, with

418 dominance by one species, compared to a much more even EcM community in
419 undisturbed forest where eight morphotypes were found. There was also an indication
420 that EcMs in the unburnt forest were concentrated in the surface soil layer, but were
421 more evenly distributed in the soil in the moderately fire-affected site. Several reasons
422 for severe reduction in EcMs in burnt forests include changed microclimate, changes in
423 the input of leaf litter, volatilization of organically bound nutrients, the death of host
424 trees, and possible sterilization of upper layers of the soil by the fires (Certini 2005)
425
426 REPONSES TO LOGGING DISTURBANCE.— Initial fruit body data from Pasoh showed
427 slightly more EcM species in logged (98) than unlogged (75) forest (largely due to more
428 *Russula* species), although only around 10 percent of species were shared by both forest
429 types (Watling *et al*. 1998). Additional data revealed that logged forests contained only
430 32 percent of the fungal flora of the forest reserve as a whole (Watling *et al*. 2002),
431 although this number is difficult to put into context given the differences in area and
432 sampling effort between the logged and unlogged forests. Lee *et al*. (1996b) found no
433 difference in percentage EcM on *Hopea nervosa* and *Shorea leprosula* in recently
434 logged (up to three yr previously) and unlogged plots at Danum Valley, Sabah, and the
435 number of EcM morphotypes on the roots of the seedlings showed no consistent
436 patterns across the three paired sites studied. Of the 61 EcM morphotypes, 30 were
437 exclusive to unlogged forest whereas 16 were restricted to logged forest; furthermore, of
438 29 EcM morphotypes which were found only in one of the sixteen plots, around three-
439 quarters of these were found in unlogged forest only, suggesting that logging may have
440 more of a negative impact on uncommon EcM morphotypes. Ingleby *et al*. (1998)
441 examined EcMs on *Shorea parvifolia* nine months after hand logging and found an
442 increased diversity of EcM morphotypes under the logged, higher irradiance conditions.

However, in this study it is difficult to disentangle the effects of logging from increased light levels created by logging disturbance. The immediate impacts of logging on the diversity and functioning of the EcM communities has not yet been assessed.

COLONIZATION BY OTHER (SYMBIOTIC) FUNGAL STRUCTURES

There are reports of some dipterocarps also forming arbuscular mycorrhiza (AM) associations (Shamsudin 1979, Chalermpongse 1987, Ibrahim *et al*. 1995, Dhungana *et al*. 1996, Shi *et al*. 2002, 2007; Tawaraya *et al*. 2003) and an important question is how common is dual colonization, and are interactions among colonisers beneficial to the host plants, as seen by Chen *et al*. (2000) for eucalypts? The only data on dual colonization did not find a difference in the relative growth rate of *Hopea odorata* seedlings with EcM alone (38 out of 54 seedlings) or dual EcM/AM colonization (16 out of 54 seedlings) (Ibrahim *et al*. 1995). Ectendomycorrhizal colonization has also been reported in *Shorea parvifolia* (Louis 1988) and other dipterocarps (Chalermpongse 1987, Tupas and Sajise 1976). All of the above information suggests that there could be a considerable diversity of mycorrhizal morphologies in the Dipterocarpaceae, and additional morphological information on mycorrhizal symbioses is needed.

FUTURE WORK

Increased knowledge of dipterocarp-associated EcM fungal community structure is being facilitated by extensive and long-term fruiting body surveys as well as molecular analyses of belowground EcM communities. Nursery and field based studies are improving understanding of growth and nutrition relations of EcM dipterocarp seedlings (Brearley 2011). The following areas for future research on dipterocarp-associated EcM fungi and plant-fungal ecosystem interactions are suggested:

(1) Bring more EcM fungi into culture and test them for functional symbiotic capabilities. Fungi that appear to promote plant performance should be further investigated in field studies where the ecological importance of EcM for dipterocarp growth and survival is most important although currently equivocal.

(2) It is important to determine the roles that fungi might be playing in ecosystem nutrient cycling processes. How do they influence leaf litter decomposition and the subsequent release of nutrients? This might be achieved by analyses of extracellular enzyme activities. Do EcMs influence ecosystem processes? A nitrogen isotopic budget of ecosystem compartments might shed some light on the importance of EcM fungi in nitrogen-cycling processes (see Hobbie & Hobbie 2008).

(3) Community studies on EcM root tips and fruiting bodies are needed, as are studies of community dynamics in response to land-use change or other current global changes. Our understanding of EcM responses to logging remains rudimentary, and it is not clear which species or groups of species are more or less affected by disturbances. Although some studies have suggested that temperate and tropical EcM communities have similar diversity, tropical studies are mostly short term and have not examined, for example, differentiation by depth or seasonal changes. Linking fungal diversity with ecosystem processes in tropical forests, and how such relationships are affected by disturbances is another area of considerable research importance..

(4) Taxonomic capacity for fungal studies in the appropriate geographical regions needs to be improved, for both traditional taxonomy as well as molecular taxonomy. Herbaria

493 provide a valuable repository of sequence diversity (*e.g.,* Brock *et al*. 2008) and
494 sequences from identified fungal fruit body specimens would allow us to relate
495 belowground to aboveground fungal diversity in a more meaningful way.
496
497 (5) We should be determining the ecophysiological requirements of selected
498 functionally important tropical EcM isolates. Other than those studies on species of
499 interest for inoculation schemes (Patahayah *et al*. 2003, Brearley *et al*. 2005) there is
500 minimal knowledge on the ecophysiology of tropical EcM fungi. For example, what are
501 their temperature and nutrient requirements? Can they access organic nutrients, as has
502 been shown in temperate regions?
503
504 (6) And finally, what is the morphological diversity of mycorrhizal types? Is dual
505 mycorrhizal colonization common and functionally important? If so, what are the
506 developmental, physiological and environmental factors in controlling potential dual
507 colonization?
508
509 **ACKNOWLEDGMENTS**
510 I thank the British Ecological Society for funding my Ph.D. research on dipterocarp
511 ectomycorrhizas in Sabah, Malaysia (1999–2003) and Dr. Lee Su See and her staff for
512 collaboration and support of my current research in Peninsular Malaysia (2009
513 onwards). David Burslem, Jaboury Ghazoul, Bernard Moyersoen and two anonymous
514 reviewers provided helpful comments that improved the manuscript.
515
516
517

518 **LITERATURE CITED**

519 AKEMA, T., I. NURHIFTISNI, SUCIATMIH, AND H. SIMBOLON. 2009. The impact of the
520 1998 forest fire on ectomycorrhizae of dipterocarp trees and their recovery in
521 tropical forests of East Kalimantan, Indonesia. JARQ 43: 137-143.
522 ALBRECHT, C., T. BURGESS, B. DELL, AND F. F. LAPEYRIE. 1994. Chitinase and
523 peroxidase activities are induced in eucalyptus roots according to aggressiveness
524 of Australian ectomycorrhizal strains of *Pisolithus* sp. New Phytol. 127: 217-222.
525 ALEXANDER, I. J. 2006. Ectomycorrhizas – out of Africa? New Phytol. 172: 589-591.
526 ALEXANDER, I. J., AND P. HÖGBERG. 1986. Ectomycorrhizas of tropical angiospermous
527 trees. New Phytol. 102: 541-549.
528 ALEXANDER, I. J., A. NORANI, AND S. S. LEE. 1992. The role of mycorrhizas in the
529 regeneration of some Malaysian forest trees. *In* A. G. Marshall and M. D. Swaine
530 (Eds.). Tropical Rain Forest: Disturbance and Recovery, pp. 357-367. The Royal
531 Society, London, UK.
532 BAILLIE, I. C., P. S. ASHTON, S. P. CHIN, S. J. DAVIES, P. A. PALMIOTTO, S. E. RUSSO,
533 AND S. TAN. 2006. Spatial association of humus, nutrients and soil in mixed
534 dipterocarp forest at Lambir, Sarawak, Malaysian Borneo. J. Trop. Ecol. 22: 543-
535 553.
536 BAUM, C., AND F. MAKESCHIN. 2000. Effects of nitrogen and phosphorus fertilization on
537 mycorrhizal formation of two poplar clones (*Populus trichocarpa* and *P. tremula x*
538 *tremuloides*). J. Plant Nutr. Soil Sci. 163: 491-497.
539 BECKER, P. 1983. Ectomycorrhizas on *Shorea* (Dipterocarpaceae) seedlings in a
540 lowland Malaysian rainforest. Malay. For. 46: 146-170.
541 BÉREAU, M., M. GAZEL, AND J. GARBAYE. 1997. Les symbioses mycorhiziennes des
542 arbres de la forêt tropicale humide de Guyana française. Can. J. Bot. 75: 711-716.

543 BEIMFORDE, C., N. SCHÄFER, H. DÖRFELT, P. C. NASCIMBENE, H. SINGH, J. HEINRICHS,
544 J. REITNER, R. S. RANA, AND A. R. SCHMIDT. 2011. Ectomycorrhizas from a Lower
545 Eocene angiosperm forest. New Phytol. 192 : 988-996.
546 BERRIMAN, C. P. 1986. Mycorrhizas of *Shorea* (Dipterocarpaceae) in Relation to Host
547 Specificity and Soil Phosphorus Status. B.Sc. Dissertation, University of Aberdeen,
548 UK.
549 BREARLEY, F. Q. 2003. The Role of Ectomycorrhizas in the Regeneration of
550 Dipterocarp Seedlings. Ph.D. Dissertation, University of Sheffield, UK.
551 BREARLEY, F. Q. 2006. Differences in the growth and ectomycorrhizal community of
552 *Dryobalanops lanceolata* (Dipterocarpaceae) seedlings grown in ultramafic and
553 non-ultramafic soils. Soil Biol. Biochem. 38: 3407-3410.
554 BREARLEY, F. Q. 2011. The importance of ectomycorrhizas for the growth of
555 dipterocarps and the efficacy of ectomycorrhizal inoculation schemes. *In* M. Rai and
556 A. Varma (Eds.). Diversity and Biotechnology of Ectomycorrhizae, pp. 3-17.
557 Springer-Verlag, Berlin, Germany.
558 BREARLEY, F. Q., M. C. PRESS, AND J. D. SCHOLES. 2003. Nutrients obtained from leaf
559 litter can improve the growth of dipterocarp seedlings. New Phytol. 160: 101-110.
560 BREARLEY, F. Q., S. PRAJADINATA, P. S. KIDD, J. PROCTOR, AND SURIANTATA 2004.
561 Structure and floristics of an old secondary rain forest in Central Kalimantan,
562 Indonesia, and a comparison with adjacent primary forest. For. Ecol. Manage. 195:
563 385-397.
564 BREARLEY, F. Q., J. D. SCHOLES, AND S. S. LEE. 2005. Nitrogen nutrition and isotopic
565 discrimination in tropical ectomycorrhizal fungi. Res. Microbiol. 156: 184-190.

566 BREARLEY, F. Q., J. D. SCHOLES, M. C. PRESS, AND G. PALFNER. 2007. How does light
567 and phosphorus fertilisation affect the growth and ectomycorrhizal community of
568 two contrasting dipterocarp species? Plant Ecol. 192: 237-249.
569 BROCK, P. M., H. DÖRING, AND M. I. BIDARTONDO. 2008. How to know unknown fungi:
570 the role of a herbarium. New Phytol. 181: 719-724.
571 BROOK, R. M. 1989. Review of literature on *Imperata cylindrica* (L.) Raueschel with
572 particular reference to south east Asia. Trop. Pest Manage. 35: 12-25.
573 CERTINI, G. 2005. Effects of fires on properties of forest soils: a review. Oecologia, 143:
574 1-10.
575 CHALERMPONGSE, A. 1987. Mycorrhizal survey of dry-deciduous and semi-evergreen
576 dipterocarp forest ecosystems in Thailand. *In* A. J. C. H. Kostermans (Ed.).
577 Proceedings of the Third Round Table Conference on Dipterocarps, pp.81-103.
578 UNESCO Regional Office for Science and Technology, Jakarta, Indonesia.
579 CHANG, Y. S., F. F. LAPEYRIE, AND S. S. LEE. 1994. The survival and competitiveness of
580 *Pisolithus tinctorius* on outplanted seedlings of *Shorea glauca* in Malaysia. *In* S.
581 Appanah and K. C. Khoo (Eds.). Proceedings of the Fifth Round Table Conference
582 on Dipterocarps, pp. 165-169. Forest Research Institute of Malaysia, Kepong,
583 Malaysia.
584 CHANG, Y. S., S. S. LEE, F. F. LAPEYRIE, AND S. M. YAZID. 1995. The competitiveness
585 of two strains of *Pisolithus tinctorius* on seedlings of three species of dipterocarps
586 under nursery and field conditions: preliminary results. *In* R. Wickneswari, A. Z.
587 Yahya, A. H. M. Shariff, D. Haji Ahmad, K. C. Khoo, K. Suzuki, S. Sakurai and K.
588 Ishii (Eds.). Proceedings of the International Workshop of BIO-REFOR, Kangar,
589 1994, pp. 208-212. BIO-REFOR, IUFRO-SPDC, Tokyo, Japan & Forest Research
590 Institute of Malaysia, Kepong, Malaysia.

591 CHEN, Y. L., M. C. BRUNDRETT, AND B. DELL. 2000. Effects of ectomycorrhizas and
592 vesicular-arbuscular mycorrhizas, alone or in competition, on root colonization and
593 growth of *Eucalyptus globulus* and *E. urophylla*. New Phytol. 146: 545-556.
594 CONNELL, J. H., AND M. D. LOWMAN. 1989. Low-diversity tropical rain forests: some
595 possible mechanisms for their existence. Am. Nat. 134: 88-119.
596 CORNER, E. J. H. 1972. Boletus in Malaysia. Government Printing Office, Singapore.
597 CORNER, E. J. H. 1988. Higher fungi. *In*: Earl of Cranbrook (Ed.). Key Environments:
598 Malaysia, pp. 88-101. Pergamon Press, Oxford, UK.
599 DARUSMAN, L. K. 1998. Kinetics of root chitinase during the association process
600 between *Shorea selanica* and mycorrhiza of *Scleroderma columnare*. Hayati 5: 95-
601 97.
602 DAYANANDAN, S., P. S. ASHTON, S. M. WILLIAMS, AND R. B. PRIMACK. 1999.
603 Phylogeny of the tropical tree family Dipterocarpaceae based on nucleotide
604 sequences of the chloroplast *rbcL* gene. Am. J. Bot. 86: 1182- 1190.
605 DE ALWIS, D. P., AND K. ABEYNAYAKE. 1980. A survey of mycorrhiza in some forest
606 trees in Sri Lanka. *In* P. Mikola (Ed.). Tropical Mycorrhiza Research, pp. 146-
607 153. Clarendon Press, Oxford, UK.
608 DE ALWIS, D. P., AND K. ABEYNAYAKE. 1988. Aseptic synthesis of mycorrhizae of
609 *Dipterocarpus zeylandicus*. *In* F. S. P. Ng (Ed.). Trees and Mycorrhiza:
610 Proceedings of the Asian Seminar pp. 215-226. Forest Research Institute of
611 Malaysia, Kepong, Malaysia.
612 DE VOOGD, C. N. A. 1933. Cultuurproeven met Shorea platyclados v. Sl. in Redjang en
613 Lebong. Tectona 26: 703-713.
614 DEACON, J. W., S. D. DONALDSON, AND F. T. LAST. 1983. Sequences and interactions of
615 mycorrhizal fungi on birch. Plant Soil 71: 257-262.

616 DHUNGANA, H. N., D. DUTTA, G. S. SARMA, AND P. HAZARIKA. 1996. Occurrence of
617 vesicular-arbuscular mycorrhizae in seedlings of some forest tree species. J. Trop.
618 For. 12: 156-158.
619 DUCOUSSO, M., G. BÉNA, C. BOURGEOIS, B. BUYCK, G. EYSSARTIER, M. VINCELETTE, R.
620 RABEVOHITRA, L. RANDRIHASIPARA, B. DREYFUS, AND Y. PRIN. 2004. The last
621 common ancestor of Sarcolaenaceae and Asian dipterocarp trees was
622 ectomycorrhizal before the India-Madagascar separation, about 88 million years
623 ago. Mol. Ecol. 13: 231-236.
624 EYSSARTIER, G., D. STUBBE, R. WALLEYN, AND A. VERBEKEN. 2009. New records of
625 *Cantharellus* (Basidiomycota, *Cantharellaceae*) from Malaysian dipterocarp
626 rainforest. Fungal Div. 36: 57-67.
627 HADI, S., AND E. SANTOSO. 1988. Effect of *Russula* spp., *Scleroderma* sp. and *Boletus*
628 sp. on the mycorrhizal development and growth of five dipterocarp species. *In* M.
629 Mohinder Singh (Ed.). Agricultural and Biological Research Priorities in Asia,
630 Proceedings of the IFS Symposium of Science Asia 87, pp. 183-185. International
631 Foundation for Science & Malaysian Scientific Association, Kuala Lumpur,
632 Malaysia.
633 HADI, S., AND E. SANTOSO. 1989. Accumulation of macronutrients by five dipterocarp
634 species inoculated with different species of mycorrhizal fungi. *In* A. Mahadevan, N.
635 Raman and K. Natarajan (Eds.). Mycorrhizae for Green Asia: Proceedings of the
636 First Asian Conference on Mycorrhizae, pp.139-141. Centre for Advanced Studies
637 on Botany, University of Madras, India.
638 HAWKSWORTH, D. L. 1993. The tropical fungal biota: census, pertinence, prophylaxis,
639 and prognosis. *In* S. Isaac, J. C. Frankland, R. Watling and A. J. S. Whalley (Eds.).
640 Aspects of Tropical Mycology, pp. 265-293. Cambridge University Press, UK.

641 HENKEL, T. W. 2003. Monodominance in the ectomycorrhizal *Dicymbe corymbosa*
642 (Caesalpiniaceae) from Guyana. J. Trop. Ecol. 19: 417-437.
643 HENKEL, T. W., M. C. AIME, M. M. L. CHIN, S. L. MILLER, R. VILGALYS AND M. E.
644 SMITH. In press. Ectomycorrhizal fungal sporocarp diversity and discovery of new
645 taxa in *Dicymbe* monodominant forests of the Guiana Shield. Biodivers. Conserv.
646 HOBBIE, E. A., AND J. E. HOBBIE. 2008. Natural abundance of ^{15}N in nitrogen-limited
647 forests and tundra can estimate nitrogen cycling through mycorrhizal fungi: a
648 review. Ecosystems 11: 815-830.
649 HONG, L. T. 1979. A note on dipterocarp mycorrhizal fungi. Malay. For. 42: 280-283.
650 IBRAHIM, Z., M. N. MAHAT, AND S. S. LEE. 1995. Response of *Hopea odorata* seedlings
651 to biological soil conditioners. *In* R. Wickneswari, A. Z. Yahya, A. H. M. Shariff,
652 D. Haji Ahmad, K. C. Khoo, K. Suzuki, S. Sakurai and K. Ishii (Eds.). Proceedings
653 of the International Workshop of BIO-REFOR, Kangar, 1994, pp.179-182. BIO-
654 REFOR, IUFRO-SPDC, Tokyo, Japan & Forest Research Institute of Malaysia,
655 Kepong, Malaysia.
656 INGLEBY, K. 1999. Inocybe avellana Horak + Shorea leprosula Miq. *In* R. Agerer, R. M.
657 Danielson, S. Egli, K. Ingleby, D. Luoma and R. Treu (Eds.). Descriptions of
658 Ectomycorrhizae, Volume **4**, pp. 55-60. Einhorn-Verlag, Schwäbisch Gmünd,
659 Germany.
660 INGLEBY, K., R. C. MUNRO, M. NOOR, P. A. MASON, AND M. J. CLEARWATER. 1998.
661 Ectomycorrhizal populations and growth of *Shorea parvifolia* (Dipterocarpaceae)
662 seedlings regenerating under three different forest canopies following logging. For.
663 Ecol. Manage. 111: 171-179.

664 INGLEBY, K., L. T. T. THUY, N. T. PHONG, AND P. A. MASON. 2000. Ectomycorrhizal
665 inoculum potential of soils from forest restoration sites in south Vietnam. J. Trop.
666 For. Sci. 12: 418-422.
667 IRINO, K. O., Y. IBA, S. ISHIZUKA, T. KENZO, S. RIPOT, J. J. KENDAWANG, N. MIYASHITA,
668 K. NARA, T. HOGETSU, I. NINOMIYA, K. IWASAKI, AND K. SAKURAI. 2004. Effects of
669 controlled-release fertilizer on growth and ectomycorrhizal colonization of pot-
670 grown seedlings of the dipterocarp *Dryobalanops lanceolata* in a tropical nursery.
671 Soil Sci. Plant Nutr. 50: 747-753.
672 IWAMOTO, K., AND K. KITAYAMA. 2002. Abundances of ectomycorrhizas on the slopes
673 of Mount Kinabalu, Sabah, Malaysian Borneo. Sabah Park. Nat. J. 5: 239-255.
674 JONES, M. D., D. M. DURALL, AND P. B. TINKER. 1990. Phosphorus relationships and
675 production of extramatrical hyphae by two types of willow ectomycorrhizas at
676 different soil phosphorus levels. New Phytol. 115: 259–267
677 JÜLICH, W. 1985. Fungi associated with Dipterocarpaceae in Southeast Asia. 1. The
678 genera *Riessia* and *Riessiella*. Int. J. Mycol. Lichenol. 2: 123-140.
679 KETTLE, C. J. 2010. Ecological considerations for using dipterocarps for restoration of
680 lowland rainforest in Southeast Asia. Biodivers. Conserv. 19: 1137-1151.
681 LEE, S. S. 1998. Root symbiosis and nutrition. *In* S. Appanah and J. M. Turnbull (Eds.).
682 A Review of Dipterocarps: Taxonomy, Ecology and Silviculture, pp. 99-114.
683 Centre for International Forestry Research, Bogor, Indonesia.
684 LEE, S. S. 2005. Macrofungal diversity in Peninsular Malaysia focusing on the
685 ectomycorrhizal fungi. Clusiana 44: 57-66.
686 LEE, S. S., AND I. J. ALEXANDER. 1994. The response of seedlings of two dipterocarp
687 species to nutrient additions and ectomycorrhizal infection. Plant Soil 163: 299-
688 306.

LEE, S. S., AND I. J. ALEXANDER. 1996. The dynamics of ectomycorrhizal infection of *Shorea leprosula* seedlings in Malaysian rain forests. New Phytol. 132: 297-305.

LEE, S. S., AND K. L. LIM. 1989. Mycorrhizal infection and foliar phosphorus content of seedlings of three dipterocarp species grown in selectively logged forest and a forest plantation. Plant Soil, 117: 237-241.

LEE, S. S., AND M. PATAHAYAH. 2003. Host specificity of dipterocarp ectomycorrhizal fungi. *In* H. Aminah, S. Ani, H. C. Sim and B. Krishnapillay (Eds.). Proceedings of the Seventh Round-Table Conference on Dipterocarps. 7-10 October 2002, pp. 214-217. Asia Pacific Association of Forestry Research Institutions, Kuala Lumpur, Malaysia.

LEE, S. S., H. BESL, AND S. UJANG. 1995a. Some fungi of the Sungai Halong and surrounding areas, Temengor Forest Reserve, Hulu Perak, Malaysia. Malay. Nat. J. 48: 147-155.

LEE, S. S., F. F. LAPEYRIE AND S. M. YAZID. 1995b. Techniques for controlled ectomycorrhizal inoculation of dipterocarp seedlings and cuttings. *In* Supriyanto and J. T. Kartana (Eds.). Proceedings of the Second Symposium on Biology and Biotechnology of Mycorrhizae and Third Asian Conference on Mycorrhizae (ACOM III), BIOTROP Special Publication 56, pp.217-221. SEAMEO BIOTROP, Bogor, Indonesia.

LEE, S. S., R. WATLING, AND E. TURNBULL. 1996a. Ectomycorrhizal fungi as possible bio-indicators in forest management. *In* N. Hussein, P. S. Bacon and K. C. Khoo (Eds.). Forestry and Forest Products Research: Proceedings of the Third Conference, Volume 1, pp. 63-68. Forest Research Institute of Malaysia, Kepong, Malaysia.

LEE, S. S., I. J. ALEXANDER, P. H. MOURA-COSTA, AND S. W. YAP. 1996b. Mycorrhizal infection of dipterocarp seedlings in logged and undisturbed forests. *In* S. Appanah and K. C. Khoo (Eds.). Proceedings of the Fifth Round Table Conference on Dipterocarps, pp. 157-164. Forest Research Institute of Malaysia, Kepong, Malaysia.

LEE, S. S., I. J. ALEXANDER, AND R. WATLING. 1997. Ectomycorrhizas and putative ectomycorrhizal fungi of *Shorea leprosula* Miq. (Dipterocarpaceae). Mycorrhiza 7: 63-81.

LEE, S. S., R. WATLING, AND Y. NORAINI SIKIN. 2002a. Ectomycorrhizal basidiomata fruiting in lowland rain forests of peninsular Malaysia. Bois Fôr. Trop. 274(4): 33-43.

LEE, S. S., M. PATAHAYAH, AND F. F. LAPEYRIE. 2002b. Exotic vs. indigenous ectomycorrhizal fungi for inoculation of dipterocarps. In K. Ishii, M. Matsumori and K. Suzuki (Eds.). BIO-REFOR: Proceedings of Tokyo-Workshop, pp. 84-87. BIO-REFOR, IUFRO-SPDC, Tokyo, Japan.

LEE, S. S., R. WATLING, AND E. TURNBULL. 2003. Diversity of putative ectomycorrhizal fungi in Pasoh Forest Reserve. *In* T. Okuda, N. Manokaran, Y. Matsumoto, K. Niiyama, S. C. Thomas and P. S. Ashton (Eds.). Pasoh: Ecology of a Lowland Rain Forest in Southeast Asia, pp. 149-159. Springer-Verlag, Tokyo, Japan.

LEE, S. S., M. PATAHAYAH, W. S. CHONG, AND F. F. LAPEYRIE. 2008. Successful ectomycorrhizal inoculation of two dipterocarp species with a locally isolated fungus in Peninsular Malaysia. J. Trop. For. Sci. 20: 237-247.

LEE, S. S., B. K. THI, AND M. PATAHAYAH. 2010. An ectomycorrhizal Thelephoroid fungus of Malaysian dipterocarp seedlings. J. Trop. For. Sci. 22: 355-363.

LEPAGE, B. A., R. S. CURRAH, R. A. STOCKEY, AND G. W. ROTHWELL. 1997. Fossil ectomycorrhizae from the middle Eocene. Am. J. Bot., 84: 410-412.

LIANG, Y., L.-D. GUO, AND K.-P. MA. 2004. Genetic structure of a population of the ectomycorrhizal fungus *Russula vinosa* in subtropical woodlands in southwest China. Mycorrhiza 14: 235-240.

LÓPEZ-QUINTERO, C. A., G. STRAATSMA, A. E. FRANCO-MOLANO, AND T. BOEKHOUT. in press. Macrofungal diversity in Colombian Amazon forests varies with regimes of disturbance. Biodivers. Conserv.

LOUIS, I. 1988. Ecto- and ectendomycorrhizae in the tropical dipterocarp, *Shorea parvifolia*. Mycologia 80: 845-849.

LOUIS, I., AND E. SCOTT. 1987. In vitro synthesis of mycorrhiza in root organ cultures of a tropical dipterocarp species. Trans. Br. Mycol. Soc. 88: 565-568.

MCGUIRE, K. L. 2007. The common ectomycorrhizal net may maintain monodominance in a tropical rain forest. Ecology 88: 567-574.

MCGUIRE, K. L., T. W. HENKEL, I. GRANZOW DE LA CERDA, G. VILLA, F. EDMUND, AND C. ANDREW. 2008. Dual mycorrhizal colonization of forest-dominating tropical trees and the mycorrhizal status of non-dominant tree and liana species. Mycorrhiza 18: 217-222.

MOLINA, R., H. B. MASSICOTTE, AND J. M. TRAPPE. 1992. Specificity phenomena in mycorrhizal symbioses: community ecological consequences and practical applications. *In* M. F. Allen (Ed.). Mycorrhizal Functioning: an Integrative Plant-Fungal Process, pp. 357-423. Chapman & Hall, New York, USA.

MOYERSOEN, B. 1993. Ectomicorrizas y micorrizas vesículares-arbusculares en Caatinga Amazónica. Scientia Guaianæ 3, Caracas, Venezuala.

761 MOYERSOEN, B. 2000. Diversity of ectomycorrhizal fungi associated with four species
762 and two genera of Dipterocarpaceae in a field and bioessay experiment in Brunei
763 Darussalam. *In* Anon. (Ed.). Tropical Mycology 2000 Abstracts, p. 25. British
764 Mycological Society, London, UK.
765 MOYERSOEN, B. 2006. *Pakaraimaea dipterocarpacea* is ectomycorrhizal, indicating an
766 ancient Gondwanaland origin for the ectomycorrhizal habit in Dipterocarpaceae.
767 New Phytol. 172: 753-762.
768 NATARAJAN, K., G. SENTHILARASU, V. KUMARESAN, AND T. RIVIÈRE. 2005. Diversity in
769 ectomycorrhizal fungi of a dipterocarp forest in Western Ghats. Curr. Sci. 88:
770 1893-1895.
771 NEWBERY, D. MCC., I. J. ALEXANDER, D. W. THOMAS, AND J. S. GARTLAN. 1988.
772 Ectomycorrhizal rainforest legumes and soil phosphorus in Korup National Park,
773 Cameroon. New Phytol. 109: 433-450.
774 NEWMAN, M. F., P. F. BURGESS, AND T. C. WHITMORE. 1996. Manuals of Dipterocarps
775 for Foresters: Borneo Island Light Hardwoods. Royal Botanic Garden, Edinburgh,
776 UK.
777 NEWMAN, M. F., P. F. BURGESS, AND T. C. WHITMORE. 1998. Manuals of Dipterocarps
778 for Foresters: Borneo Island Medium and Heavy Hardwoods. Royal Botanic
779 Garden, Edinburgh, UK.
780 NEWSHAM, K. K., A. H. FITTER, AND A. R. WATKINSON. 1995. Multi-functionality and
781 biodiversity in arbuscular mycorrhizas. TREE 10: 407-411.
782 PALMIOTTO, P. A., S. J. DAVIES, K. A. VOGT, P. M. S. ASHTON, D. J. VOGT, AND P. S.
783 ASHTON. 2004. Soil-related habitat specialization in dipterocarp rain forest tree
784 species in Borneo. J. Ecol. 92: 609-623.

785 PAOLI, G. D., L. M. CURRAN, AND D. R. ZAK. 2006. Soil nutrients and beta diversity in
786 the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain
787 forest trees. J. Ecol., 94: 157-170.
788 PATAHAYAH, M., P. C. CYNTHIA, AND S. S. LEE. 2003. Optimizing growth conditions for
789 ectomycorrhizal inoculum production of the Malaysian strain of *Pisolithus*
790 *tinctorius*. *In* A. H. Mohamed, I. H. Parlan, S. Ibrahim, S. Y. M. Yussof, H. F.
791 Lim, M. A. M. Idris, A. R. A. Ghani, S. Ujang and K. A. Hamzah (Eds.). Tropical
792 Forestry Research in the New Millennium: Meeting Demands and Challenges.
793 Proceedings of the International Conference on Forestry and Forest Products
794 Research (CFFPR 2001), pp. 551-552. Asia Pacific Association of Forestry
795 Research Institutions & Forest Research Institute of Malaysia, Kuala Lumpur,
796 Malaysia.
797 PEAY, K. G., P. G. KENNEDY, S. J. DAVIES, S. TAN, AND T. D. BRUNS. 2010. Potential
798 link between plant and fungal distributions in a dipterocarp rainforest: community
799 and phylogenetic structure of tropical ectomycorrhizal fungi across a plant and
800 soil ecotone. New Phytol. 185: 529-542.
801 PEGLER, D. N. 1997. The Larger Fungi of Borneo. Natural History Publications, Kota
802 Kinabalu, Malaysia.
803 PEH K. S.-H., S. L. LEWIS, AND J. LLOYD. 2011. Mechanisms of monodominance in
804 diverse tropical tree-dominated systems. J. Ecol. 99: 891-898.
805 PEYRONEL, B., AND B. FASSI. 1957. Micorrize ectotrofiche in una Caesalpinacea del
806 Congo Belga. Atti Accad. Sci. Torino 91: 569-576.
807 PHOSRI, C., S. PÕLME, A. F. S. TAYLOR, U. KÕLJALG, N. SUWANNASAI, AND L.
808 TEDERSOO. in press. Diversity and community composition of ectomycorrhizal
809 fungi in a dry deciduous dipterocarp forest in Thailand. Biodivers. Conserv.

PROCTOR, J., J. M. ANDERSON, P. CHAI, AND H. W. VALLACK. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. J. Ecol. 71: 237-260.

READ, D. J. 1986. Non-nutritional effects of mycorrhizal infection. *In* V. Gianinazzi-Pearson and S. Gianiniazzi (Eds.) Physiological and Genetical Aspects of Mycorrhizae, pp. 169-176. INRA, Paris, France.

READ, D. J. 1998. Mycorrhiza - the state of the art. In A. Varma and B. Hock (Eds.). Mycorrhiza Structure, Function, Molecular Biology and Biotechnology, 2nd Edition, pp. 3-34. Springer-Verlag, Berlin, Germany.

READ, D. J. 1999. The ecophysiology of mycorrhizal symbioses with special reference to impacts upon plant fitness. *In* M. C. Press, J. D. Scholes and M. G. Barker (Eds.). Physiological Plant Ecology, pp. 133-151. Blackwell Scientific, Oxford, UK.

REDECKER, D., T. M. SZARO, R. J. BOWMAN, AND T. D. BRUNS 2001. Small genets of *Lactarius xanthogalactus*, *Russula cremoricolor* and *Amanita francheti* in late-stage ectomycorrhizal successions. Mol. Ecol. 10: 1025-1034.

RIVIÈRE, T., K. NATARAJAN, AND B. DREYFUS. 2006. Spatial distribution of ectomycorrhizal Basidiomycete *Russula* subsect. Foetentinae populations in a primary dipterocarp rainforest. Mycorrhiza 16: 143-148.

ROY, M., S. WATTANA, A. STIER, F. RICHARD, S. VESSABUTR, AND M.-A. SELOSSE 2009. Two mycoheterotrophic orchids from Thailand tropical dipterocarpaceaen forests associate with a broad diversity of ectomycorrhizal fungi. BMC Biol. 7: 51.

SANER, P. G. 2009. Ecosystem Carbon Dynamics in Logged Forests of Malaysian Borneo. Ph.D. Dissertation, University of Zurich, Switzerland.

834 SANER, P. G., C. PHILIPSON, R. C. ONG, N. MAJALAP, S. EGLI, AND A. HECTOR. 2011.
835 Positive effects of ectomycorrhizal colonization on growth of seedlings of a
836 tropical tree across a range of forest floor light conditions. Plant Soil, 338: 411-
837 421.
838 SANTOSO, E. 1988. Pengaruh mikoriza terhadap diameter batang dan bobot kering
839 anakan Dipterocarpaceae. Bul. Penelit. Hutan (504): 11-21.
840 SANTOSO, E. 1991. Pengaruh beberapa fungi mikoriza terhadap penyerapan unsur hara
841 pada lima jenis Dipterocarpaceae. Bul. Penelit. Hutan (532): 11-18.
842 SHAMSUDDIN, M. N. 1979. Mycorrhizas of tropical forest trees. *In* J. I. Furtado (Ed.).
843 Abstracts: Fifth International Symposium of Tropical Ecology, p. 173. University
844 of Malaya, Kuala Lumpur, Malaysia.
845 SHI, Z. Y., Y. L. CHEN, AND R. J. LIU. 2002. Preliminary survey on arbuscular
846 mycorrhizas of Dipterocarpaceae. Mycosystemia, 22: 82-87.
847 SHI, Z. Y., F. Y. WANG, Y. L. WEI, AND Y. L. CHEN. 2007. Observations on arbuscular
848 mycorrhizas on Dipterocarpaceae grown in tropical rainforest in China. Am.-
849 Eurasian J. Agric. Environ. Sci. 2: 247-254.
850 SHIVA, M. P., AND I. JANTAN. 1998. Non-timber forest products from dipterocarps. *In* S.
851 Appanah and J. M. Turnbull (Eds.). A Review of Dipterocarps: Taxonomy,
852 Ecology and Silviculture, pp. 187-197. Centre for International Forestry Research,
853 Bogor, Indonesia.
854 SIMARD, S. W., D. A. PERRY, M. D. JONES, D. D. MYROLD, D. M. DURALL, AND R.
855 MOLINA. 1997. Net transfer of carbon between ectomycorrhizal tree species in the
856 field. Nature 388: 579-582.
857 SIMS, K. P., R. WATLING, AND P. JEFFRIES. 1995. A revised key to the genus
858 *Scleroderma*. Mycotaxon, 56: 403-420.

SINGH, K. G. 1966. Ectotrophic mycorrhiza in equatorial rain forests. Malay. For. 29: 13-18.

SIRIKANTARAMAS, S., N. SUGIOKA, S. S. LEE, L. A. MOHAMED, H. S. LEE, A. E. SZMIDT, AND T. YAMAZAKI. 2003. Molecular identification of ectomycorrhizal fungi associated with Dipterocarpaceae. Tropics 13: 69-77.

SLIK, J. W. F., N. RAES, S.-I. AIBA, F. Q. BREARLEY, C. H. CANNON, E. MEIJAARD, H. NAGAMASU, R. NILUS, G. D. PAOLI, A. D. POULSEN, D. SHEIL, E. SUZUKI, J. L. C. H. VAN VALKENBURG, C. O. WEBB, P. WILKIE, AND S. WULFFRAAT. 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. Divers. Distrib. 15: 523-532.

SMITH, S. E., AND D. J. READ. 2008. Mycorrhizal Symbiosis, 3rd Edition. Academic Press, San Diego, USA.

SMITS, W. T. M. 1983. Dipterocarps and mycorrhiza - an ecological adaptation and a factor in forest regeneration. Flora Males. Bull. 36: 3926-3937.

SMITS, W. T. M. 1985. Specificity of dipterocarp mycorrhiza. *In* R. Molina (Ed.). Proceedings of the 6th North American Conference on Mycorrhizae, p. 364. Forest Research Laboratory, Corvallis, Oregon, USA.

SMITS, W. T. M. 1994. Dipterocarpaceae: Mycorrhizae and Regeneration. The Tropenbos Foundation, Wageningen, The Netherlands.

ST. JOHN, T. V. 1980. A survey of mycorrhizal infection in an Amazonian rain forest. Acta Amazon. 10: 527–533.

SUHARDI. 2000. Treatment to development mycorrhizal formation on dipterocarp seedlings. *In* E. Guhardja, M. Fatawi, M. Sutisna, T. Mori and S. Ohta (Eds.) Rainforest Ecosystems of East Kalimantan: El Niño, Drought, Fire and Human Impacts, Ecological Studies 140. pp. 245-250. Springer-Verlag, Tokyo, Japan.

884 SUHARDI, A. DARMAWAN, AND E. FARIDAH. 1993. Effect of shading, fertilizer and
885 mulching with alang-alang to the early growth and mycorrhiza formation of
886 *Shorea bracteolata* in Bukit Suharto. *In* Anon. (Ed.). BIO-REFOR: Proceedings
887 of Tsukuba-Workshop, pp. 161-173. BIO-REFOR, IUFRO-SPDC, Tsukuba
888 Science City, Japan.
889 TATA, M. H. L., S. HADI, C. KUSMANA, AND ACHMAD (2003) Effect of forest fire on the
890 survival of ectomycorrhizal fungi on dipterocarps. *In* H. Aminah, S. Ani, H. C.
891 Sim and B. Krishnapillay (Eds.). Proceedings of the Seventh Round-Table
892 Conference on Dipterocarps. 7-10 October 2002, pp. 173-178. Asia Pacific
893 Association of Forestry Research Institutions. Kuala Lumpur, Malaysia.
894 TATA M. H. L., M. VAN NOORDWIJK, R. SUMMERBELL, AND M. J. A. WERGER. 2010.
895 Limited response to nursery-stage mycorrhiza inoculation of *Shorea* seedlings
896 planted in rubber agroforest in Jambi, Indonesia. New For. 39: 51-74.
897 TAYLOR, A. F. S. 2002. Fungal diversity in ectomycorrhizal communities: sampling
898 effort and species detection. Plant Soil 244: 19-28.
899 TAWARAYA, K., Z. TAKAYA, M. TURJAMAN, S. J. TUAH, S. H. LIMIN, Y. TAMAI, J. Y.
900 CHA, T. WAGATSUMA, AND M. OSAKI. 2003. Arbuscular mycorrhizal colonization of
901 tree species grown in peat swamp forests of Central Kalimantan, Indonesia. For.
902 Ecol. Manage. 182: 381-386.
903 TEDERSOO, L., AND K. NARA. 2010. General latitudinal gradient of biodiversity is
904 reversed in ectomycorrhizal fungi. New Phytol. 185: 351-354.
905 TEDERSOO, L., T. SUVI, K. BEAVER, AND U. KÕLJALG. 2007a. Ectomycorrhizal fungi on
906 the Seychelles: diversity patterns and host shifts from the native *Vateriopsis*
907 *seychellarum* (Dipterocarpaceae) and *Intsia bijuga* (Caesalpinaceae) to the

introduced *Eucalyptus robusta* (Myrtaceae) but not *Pinus caribaea* (Pinaceae). New Phytol. 175: 321-333.

TEDERSOO, L., T. SUVI, K. BEAVER, AND I. SAAR. 2007b. Ectomycorrhizas of *Coltricia* and *Coltriciella* (Hymenochaetales, Basidiomycota) on Caesalpiniaceae, Dipterocarpaceae and Myrtaceae in Seychelles. Mycol. Prog. 6: 101-107.

TEDERSOO, L., T. W. MAY, AND M. E. SMITH. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20: 217-263.

TEDERSOO, L., M. BAHRAM, T. JAIRUS, E. BECHEM, S. CHINOYA, R. MPUMBA, M. LEAL, E. RANDRIANJOHANY, S. RAZAFIMANDIMBISON, A. SADAM, T. NAADEL, AND U. KÕLJALG. 2011. Spatial structure and the effects of host and soil environments on communities of ectomycorrhizal fungi in wooded savannas and rain forests of Continental Africa and Madagascar. Mol. Ecol. 20: 3071-3080.

TENNAKOON, M. M. D., I. A. U. N. GUNATILLEKE, K. M. HAFEEL, G. SENEVIRATNE, C. V. S. GUNATILLEKE, AND P. M. S. ASHTON. 2005. Ectomycorrhizal colonization and seedling growth of *Shorea* (Dipterocarpaceae) species in simulated shade environments of a Sri Lankan rain forest. For. Ecol. Manage. 208: 399-405.

TRESEDER, K. K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus and atmospheric CO_2 in field studies. New Phytol. 164: 347-355.

TUPAS, G. L., AND P. E. SAJISE. 1976. Mycorrhizal associations in some savanna and reforestation trees. Kalikasan 5: 235-240.

TURJAMAN, M., Y. TAMAI, H. SEGAH, S. H. LIMIN, J. Y. CHA, M. OSAKI, AND K. TAWARAYA. 2005. Inoculation with the ectomycorrhizal fungi *Pisolithus arhizus* and *Scleroderma* sp. improves early growth of *Shorea pinanga* nursery seedlings. New For. 30: 67-73.

933 TURJAMAN, M., Y. TAMAI, H. SEGAH, S. H. LIMIN, M. OSAKI, AND K. TAWARAYA. 2006.
934 Increase in early growth and nutrient uptake of *Shorea seminis* inoculated with two
935 ectomycorrhizal fungi. J. Trop. For. Sci. 18: 243-249.
936 TURJAMAN, M., H. SAITO, E. SANTOSO, A. SUSANTO, S. GAMAN, S. H. LIMIN, M.
937 SHIBUYA, K. TAKAHASHI, Y. TAMAI, M. OSAKI, AND K. TAWARAYA. 2007. Effect of
938 ectomycorrhizal fungi inoculated on *Shorea balangeran* under field conditions in
939 peat-swamp forests. *In* J. O. Rieley, C. J. Banks and B. Radjagukguk (Eds.).
940 Proceedings of the International Symposium and Workshop on Tropical Peatland,
941 Yogyakarta, 27-29 August 2007, pp 143-148. CARBOPEAT, University of
942 Leicester, UK.
943 TURNER, I. M., N. D. BROWN, AND A. C. NEWTON. 1993. The effect of fertilizer addition
944 on dipterocarp seedling growth and mycorrhizal infection. For. Ecol. Manage. 57:
945 329-337.
946 VAN DER HEIJDEN, M. G. A., AND I. R. SANDERS, I. R. 2002. Mycorrhizal Ecology,
947 Ecological Studies 157. Springer-Verlag, Berlin, Germany.
948 VAN GARDINGEN, P. R., M. J. CLEARWATER, T. NIFINLURI, R. EFFENDI, W.
949 RUSMANTORO, M. NOOR, P. A. MASON, K. INGLEBY, AND R. C. MUNRO. 1998.
950 Impacts of logging on the regeneration of lowland dipterocarp forest in Indonesia.
951 Commonw. For. Rev. 77: 71-82.
952 VAN ROOSENDAEL, J., AND A. THORENAAR. 1924. De natuurlijke verjonging van
953 Ngerawan (Hopea mengarawan Miq.) in zuid Sumatra. Tectona, 16: 519-567.
954 WATLING, R., AND S. S. LEE. 1995. Ectomycorrhizal fungi associated with members of
955 the Dipterocarpaceae in Peninsular Malaysia - I. J. Trop. For. Sci. 7: 657-669.
956 WATLING, R., AND S. S. LEE. 1998. Ectomycorrhizal fungi associated with members of
957 the Dipterocarpaceae in Peninsular Malaysia - II. J. Trop. For. Sci. 10: 421-430.

WATLING, R., AND S. S. LEE. 2007. Mycorrhizal mycodiversity in Malaysia. *In* E. B. G. Jones, K. D. Hyde and S. Vikineswary (Eds.). Malaysian Fungal Diversity, pp. 201-219. Mushroom Research Centre, University of Malaya & Ministry of Natural Resources and Environment, Kuala Lumpur, Malaysia,

WATLING, R., A. F. S. TAYLOR, S. S. LEE, K. SIMS, AND I. J. ALEXANDER. 1995a. A rainforest *Pisolithus*; its taxonomy and ecology. Nova Hedwig. 61: 417-429.

WATLING, R, S. S. LEE, AND E. TURNBULL. 1998. Putative ectomycorrhizal fungi of Pasoh Forest Reserve, Negri Sembilan, Malaysia. *In* S. S. Lee, Y. M. Dan, I. D. Gauld and J. Bishop (Eds.). Conservation, Management and Development of Forest Resources, pp. 96-104. Forest Research Institute of Malaysia, Kepong, Malaysia.

WATLING, R, S. S. LEE, AND E. TURNBULL. 2002. The occurrence and distribution of putative ectomycorrhizal basidiomycetes in a regenerating south-east Asian rainforest. *In* R. Watling, J. C. Frankland, A. M. Ainsworth, S. Isaac and C. H. Robinson (Eds.). Tropical Mycology: Volume 1 Macromycetes, pp. 25-43. CAB International, Wallingford, UK.

WATLING, R., S. S. LEE, AND E. TURNBULL. 2006. Notes taxonomiques et floristiques sur quelques bolets tropicaux et groupes proches. Bull. Soc. Mycol. Fr. 122: 327-352.

YASMAN, I. 1995. Dipterocarpaceae Tree-Mycorrhizae-Seedling Connections. Ph.D. Thesis, Wageningen Agricultural University, The Netherlands.

YAZID, S. M., S. S. LEE, AND F. F. LAPEYRIE. 1994. Growth stimulation of *Hopea* spp. (Dipterocarpaceae) seedlings following mycorrhizal inoculation with an exotic strain of *Pisolithus tinctorius*. For. Ecol. Manage. 67: 339-343.

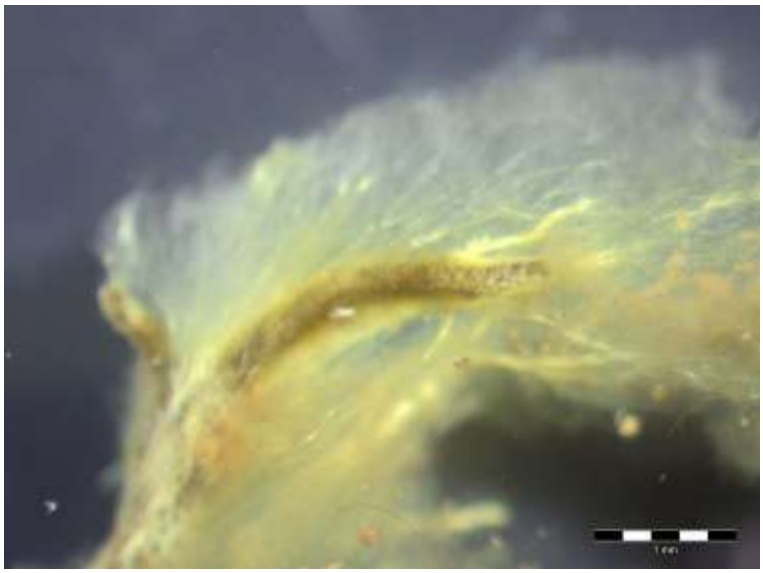
YAZID, S. M., S. S. LEE, AND F. F. LAPEYRIE. 1996. Mycorrhizal inoculation of *Hopea odorata* (Dipterocarpaceae) in the nursery. J. Trop. For. Sci. 9: 276-278.

983 YUWA-AMORNPITAK, T., T. VICHITSOONTHONKUL, M. TANTICHAROEN, S.
984 CHEEVADHANARAK, AND S. RATCHADAWONG. 2006. Diversity of ectomycorrhizal
985 fungi on Dipterocarpaceae in Thailand. J. Biol. Sci. 6: 1059-1064.
986
987

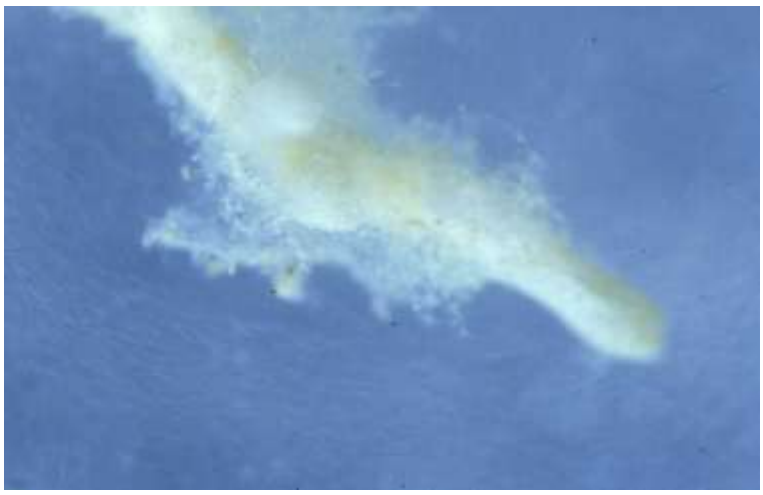
988 FIGURE 1. Ectomycorrhizas formed by A) *Scleroderma* species, B) *Inocybe* species

989 and C) Thelephorales species on roots of various member of the Dipterocarpaceae

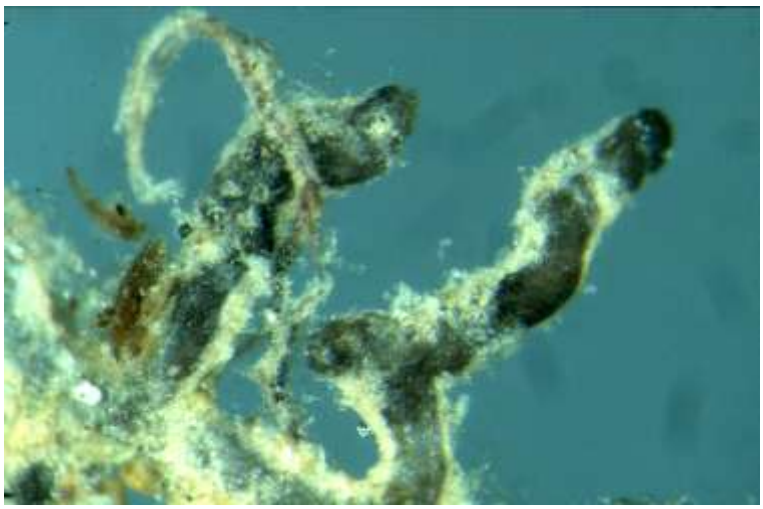
990 (*Photograph C by Götz Palfner*).



991



992



993

TABLE 1. Molecular identification of ectomycorrhizas associated with Dipterocarpaceae hosts in a number of studies. All values are the percentage of sequences found within the particular fungal lineage (taxonomic nomenclature follows Tedersoo *et al*. 2010). Note that studies are not strictly comparable due to different primer pairs used to amplify fungal DNA.

	Malaysia (Five sites)	Venezuela (*Pakaraimea dipterocarpacea*)	Thailand (Eight sites)	Seychelles (*Vateriopisis seychellarum*)	Sarawak (Lambir Hills)	Sumatra (Jambi)	Thailand (Phitsanulok)	Kalimantan (Bukit Bangkirai)
	Sirikantaramas *et al*. 2003	Moyersoen 2006	Yuwa-Amornpitak *et al*. 2006	Tedersoo *et al*. 2007a	Peay *et al*. 2010	Tata *et al.* 2010	Phosri *et al.* in press	Nara pers. comm.
Ascomycota	-	-	-	-	-	-	-	3
Elaphomycetales	-	-	-	-	1	-	4	-
Helotiales	-	-	-	-	1	-	-	-
Pezizales	-	-	-	-	-	-	3	-
Sordariales	-	-	-	11	5	-	6	-
Basidiomycota	-	-	-	-	-	-	-	-
Agaricales	-	-	3	-	3	-	-	-
/amanita	1	11	3	-	3	-	3	6
/cortinarius	1	11	-	11	10	-	-	6
/hygrophorus	1	-	-	-	-	-	-	-
/inocybe	-	22	9	6	-	-	4	2

/laccaria	-	-	-	-	-	-	1	-
Atheliales	-	-	-	-	3	-	1	-
Boletales	-	-	-	-	5	-	-	15
/boletus	17	-	6	6	11	-	1	-
/pisolithus-scleroderma	10	-	21	6	2	25	3	-
Cantharellalaes	-	-	-	-	3	-	-	11
/cantharellus	2	-	-	6	3	8	4	-
/clavulina	-	22	-	-	6	8	3	-
Hymenochaetales	-	-	-	17	2	-	-	-
Hysterangiales	-	-	-	-	1	-	-	-
Russulales	16	-	18	6	28	-	32	31
Sebacinales	-	11	-	-	2	8	6	2
Thelephorales	51	-	36	33	12	50	25	25
Unidentified	-	22	3	-	-	-	-	-